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Effect of ecological factors on fine-scale patterns of social structure in African lions

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Abstract

1. Environmental variations can influence the extent to which individuals interact with other individuals by changing the value of grouping. It is well known that many species can form and disband groups, often in response to the distribution and abundance of resources.

2. While previous studies showed that resources influence the broad-scale structure of animal groups, knowledge gaps remain on whether they affect the fine-scale patterns of association among individuals within groups.

3. We quantify association patterns in African lions while simultaneously monitoring the abundance and distribution of prey. We test how social and ecological factors, including individual trait (age, sex, reproductive state) similarity, prey availability (prey abundance, dispersion, herd size and body size), interspecific competition, and vegetation cover affect within-pride social structure in African lions.

4. In general, a greater abundance of dispersed smaller prey resulted in prides being consistently divided into subgroups with weaker cohesion among pride members. By contrast, low abundance and aggregated small herds of prey resulted in stronger connections among individuals. We found interesting trade-offs in individual decisions to associate generally (equally across all other members of the pride) when resources are aggregated and rich, and associating more exclusively (in subgroups of preferred associates) when resources are scarce. Further, lions preferentially associated equally across the pride when prey were large, providing some evidence that the composition of hunting parties might be important when prey are more

difficult to catch.

5. Our study provides evidence that ecological factors can shape both global and fine-scale properties of animal social systems, even when species live in seemingly consistently structured societies. Our findings suggest that the decisions by lions in the compromise between having few strong connections and having many weaker connections is strongly determined by ecological conditions. More broadly, our study reveals how fission-fusion dynamics and ecological factors can play out simultaneously across multiple levels of sociality.

Key words

Animal social networks, dynamic networks, ecological factors, fission-fusion, heterogeneity, lion, null models, prey availability

Introduction

One important goal in animal ecology is to understand the relationship between environmental factors and animal population abundance, spatial distribution, and social structure (Solomon 1949). Studies across different taxa have demonstrated that resource availability is an important determinant of the broad-scale structure of animal societies, with most of these studies showing that animal group size is generally larger when food resources are more abundant and of a higher quality (see Hanya & Chapman 2013; Macdonald & Johnson 2015 for reviews). In particular Nel, Loutit, Braby and Somers (2013) found that where food patches were rich, fairly clumped and heterogeneous, black-backed jackals (*Canis mesomelas*) group sizes were large and territory sizes small. In group-living animals, interactions among pairs or subgroups of individuals within a group (Hinde 1956; Macdonald, Yamaguchi &

Kerby 2000; Krause & Ruxton 2002), and the outcome of these interactions can be interpreted as a network of social relationships (Whitehead 2008; Farine & Whitehead 2015). The nature, number, and strength of these relationships are complex and can mediate the benefits, such as food sharing, that individuals accrue from living in groups, particularly in times of need (Carter, Farine & Wilkinson 2017). Earlier attempts at understanding the interactions among individuals in a carnivore social structure, using the example of farm cats (*Felis catus*), were analytically unsophisticated. However, they offered some insights into patterns of social structure of group living carnivores (see Macdonald, Apps, Carr & Kerby 1987). Modern tools in ecology and evolution are now allowing us to understand better the patterns of animal social structure (i.e. the patterns in social relationships) at a finer level of social organization (Tanner & Jackson 2012; Farine *et al.* 2015a), including in carnivores (e.g. Ellwood *et al.* 2017). Understanding the processes generating variation in social structure across populations is critical for understanding the effects of sociality (Ilany & Akçay 2016). Yet, there is still only preliminary understanding of how ecological variables shape the fine-scale patterns of animal social structure (He, Maldonado-Chaparro & Farine 2019) and the implications of these on the overall group social structure and stability.

A number of postulates have been put forward to explain social structure in different animal populations, including predation risk for explaining the grouping patterns of females in non-human primates (Sterck, Watts & van Schaik 1997), kinship for shaping spatial layout of group living animals (Hirsch, Stanton & Maldonado 2012), and homophily (individual preferences for associating with like individuals) for shaping which individuals interact most strongly (Farine 2014). Social network

analysis has been instrumental in testing these postulates. At its base, social network analysis quantifies the strength of associations or interactions among each pair of individuals in a social group or population (Whitehead 2009). It allows us to understand complex social and ecological interactions in animal communities (Croft, James & Krause 2008; Farine & Whitehead 2015) by providing metrics that quantify social structure at different levels of organization, i.e. within individuals, groups and populations. Some pioneering studies have used social network analysis to reveal details of the relationship between food availability and patterns of animal social structure. For example, Tanner and Jackson (2012) found that European shore crab (*Carcius meana*) individuals aggregated into cohesive stable subgroups when resources were clumped. Additionally, Foster *et al.* (2012) showed that when prey were abundant, the killer whale (*Orcinus orca*) population was characterized by a highly interconnected social network. Nevertheless, our understanding of the relationship between resources and social structure remains superficial. How do different aspects of food availability, such as the size and distribution of prey items, affect the finer-scale patterns of associations among individuals, in particular their decisions to form or disband subgroups?

In species that exhibit a form of fission-fusion social organization, the average size of subgroups, the amount of cohesion they show, and even their sexual composition are expected to vary depending mainly on food distribution and mating systems (Symington 1988). One species that has been widely reported as exhibiting within-group fission-fusion dynamics by forming subgroups is the African lion (*Panthera leo*) (Schaller 1972). Individuals within these subgroups form very close associations (Van Orsdol, Hanby & Bygott 1985), and subgroup membership can potentially be

influenced by the attributes of different individual lions, such as their age, sex and reproductive state. For instance, female lions often form highly stable maternity groups that are effective in defending their cubs against infanticidal males from outside the pride and subgroup (Packer, Scheel & Pusey 1990). However, the interactions between individuals within a group are also likely to vary with ecological conditions. Although lions engage in a wide variety of important social activities, such as cooperative hunting (Scheel & Packer 1991), mutual defence of kills (Cooper 1991) and cooperative defence of territory and young (Mosser & Packer 2009), it has been suggested that lion sociality might be influenced by resource availability (Macdonald, Mosser & Gittleman 2010; Mbizah, Valeix, Macdonald & Loveridge 2019). For example, habitat quality was suggested as a major driver of lion social organisation in the Serengeti National Park, Tanzania (Mosser, Fryxell, Eberly & Packer 2009), and the number of prey herds visiting a waterhole determines maximum lion group size in Hwange National Park, Zimbabwe (Valeix, Loveridge & Macdonald 2012). These studies provide evidence that the general structure of lion populations (group size) is linked to overall resource availability (food abundance).

The dynamics of resource availability especially the abundance, richness, type, and distribution of prey might also influence finer-scale lion social structure. For example, when prey are abundant, we expect that there will be less competition for food, meaning that lions will gain fewer benefits from being in larger groups. As a result, they should preferentially remain with close associates. Extensive work on baboons has shown that the strength of close associations can increase fitness (Silk *et al.* 2010; Alberts 2019). When prey are scarce, then we expect lions to associate with a greater number of their other pride members, because prey are more difficult to locate and

151 catch, and because lions become more susceptible to interspecific competition from
152 spotted hyaenas (*Crocuta crocuta*) that frequently cooperate to move lions at fresh
153 kills (Kruuk 1972). In general, group size has fitness benefits apart from resources,
154 the demands of protecting their young and themselves against encounters with
155 neighbouring prides (Packer 1986; Mosser & Packer 2009) and maintaining a long-
156 term territory (Packer *et al.* 1990; Mosser & Packer 2009) can result in lions forming
157 larger groups. Here we argue that fitness benefits might shape the tendency for
158 members of a given pride to remain cohesive or to split into smaller subgroups, which
159 is a much more flexible strategy than adding or removing members from the pride.
160 Social bonds are therefore likely to form the basis of how species such as lions
161 respond socially to ecological processes. We expect to observe a trade-off between
162 maintaining fewer but stronger bonds when conditions are good and maintaining more
163 but weaker bonds when conditions are poor and more challenging.
164
165 In this study, we combine data on the fine-scale patterns of association among
166 individuals across multiple prides of African lions with data on the prey herds in each
167 pride's territory within Hwange National Park, Zimbabwe. We consider a herd of
168 prey to represent a resource patch available to lions (Carr & Macdonald 1986), and
169 the abundance, dispersion, and richness of these patches (see Table S1) as important
170 attributes that can influence the opportunities for social interactions (Tanner &
171 Jackson 2012). Resource richness is measured by the herd size and body size of
172 mixed herds of prey. Breaking down prey availability into different axes allows us to
173 better understand the effects of prey availability on fine scale patterns of association,
174 distinguishing our study from many of its predecessors that used only prey abundance
175 as a measure of food availability.

The availability of resources is also modulate by interspecific competition and habitat structure. Spotted hyaenas are lion's main competitor, and they frequently cooperate to mob lions (Kruuk 1972) especially at fresh lion kills. Furthermore at higher hyaena to lion ratio, hyaenas can successfully seize food from lions (Lehmann *et al.* 2017). Thus, the presence of hyenas could alter or reinforce the relationship between resources and social decisions in lions. Habitat is also likely to play a role. Lions are considered ambush predators that rely heavily on concealment to catch their prey (Hopcraft, Sinclair & Packer 2005), consequently dense vegetation is important for providing cover for stalking lions which may increase their chances of prey capture (Loarie, Tambling & Asner 2013). We therefore investigate how broader ecological factors can also drive patterns of fine scale social structure by including data on the abundance of spotted hyaena and the percentage of vegetation cover in prides' territories (see Table S1).

Materials and Methods

Study area

Hwange National Park covers approximately 15 000 km^2 of semi-arid dystrophic savanna on Kalahari sands, on the north-western border of Zimbabwe. During the wet season (November to February), various waterholes, rivers and pools are rain fed and available to animals, but natural surface water then becomes scarce as the dry season progresses and only pumped waterholes (~ 50), mostly in the North of the park, maintain water availability. The end of dry season coincides with the lowest quantity and quality of browsing and grazing resources. These differences in vegetation and water distribution across the park result in differences in the distribution of herbivores

in terms of both assemblages and abundance (Chamaillé-Jammes, Charbonnel, Dray, Madzikanda & Fritz 2016). We therefore commonly distinguish three seasons in Hwange National Park: the wet season (November - February), the early dry season (March - June) and the late dry season (July - October). Lion density is estimated at around 3.5 lions/100 km^2 in the study area (Loveridge *et al.* 2016) and there is a heterogeneous distribution of prey, both spatially and temporally (Chamaillé-Jammes *et al.* 2016).

Lion pride observations

In this study, we used data from seven GPS-collared lions (two adult females and five adult males) from four different prides for the study period 2013 - 2015. Lion prides were located with the help of GPS radio-collars and at times opportunistically. The prides were observed at least five times per month to record the size and composition of their group at that time. When a group was observed, we recorded the pride name, identity of individuals present, as well as their age, sex and reproductive state (whether they had cubs). We also recorded their activities during observations and these included resting, hunting, feeding and walking. All lion individuals are recognizable by whisker patterns that are unique to each individual and natural markings such as scars, muzzle spots and tooth irregularities (Pennycuick & Rudnai 1970). We looked at two aspects of lion group (1) pride (all the individuals within a group) and (2) subgroup (individuals of a pride present at each observation). We recorded all individuals present together as being connected (Whitehead & Dufault 1999; Farine 2015). The GPS collars recorded locations every two hours day and night, and we regularly downloaded this positional data to estimate lion seasonal home range. Only individuals that had collar data with fixes covering the whole

season were included in calculating seasonal home range.

Ecological factors

To measure prey availability, we conducted multi-species spoor (tracks made by animals when they cross the roads) surveys from 2013 to 2015 during the early dry season and the late dry season. Most of the available roads in the study area were used as transects (n = 64 transects) and were between 9 and 55 km long. The 64 selected transects were within areas that lions frequent. When a fresh spoor (less than 24hrs old) was encountered, it was assessed for species and group size by highly skilled and experienced trackers (see S1 Appendix for further details on the spoor survey method). Only spoor from common lion prey species in the area was used in this analysis. Information on prey availability was extracted for each lion home range in each season (See S2 Appendix for further details). From the spoor surveys, we also extracted information on the abundance of hyaenas within lion home ranges and then calculated the ratio of hyaena abundance to lion pride size. We used a vegetation map (Arraut, Loveridge, Chamaillé-Jammes, Valls-Fox & Macdonald submitted) to calculate the percentage of vegetation cover within each lion home range. We re-classed the original seven vegetation classes into two main classes; open vegetation (grassland and bushed grassland) and closed vegetation (bushland, woodland deciduous, mopane scrubland, mopane woodland and woodland evergreen) and calculated the percentage of the closed vegetation within each lion home range.

Social networks construction

We used lion pride observational data to construct a social network for each pride in each dry season in each year, with observations ranging from 16 to 66 observations

per season (Table S3). Thus, each social network represented the patterns of associations within a pride over a four-month period. The social networks contained each of the individuals in one pride as nodes and pairwise association indices as edge weights. Because we did not have complete data on observations of all groups simultaneously, we had to convert the number of associations into an association rate (the propensity for individuals to be seen together). To calculate these edge weights, we used the Simple Ratio Index as an estimate of the proportion of time two individuals spent together (Cairns & Schwager 1987; Hoppitt & Farine 2017). The Simple Ratio Index is defined as $x / (y_a + y_b + y_{ab} + x)$, where x is the number of observations of two individuals together, y_a is the number of observations with only individual a, y_b is the number of observations with only individual b. y_{ab}, the number of simultaneous observations of individuals a and b, was not relevant to our study. This ratio ranges from 0 for two individuals never seen in the same subgroup and 1 for two individuals always seen in the same subgroup. Animals that died during a season were not included in that season's network.

Social network analysis

We first used the multiple regression quadratic assignment procedure (MRQAP) to test if the tendency of lions to associate with individuals of the same sex, same age or same reproductive state had an effect on lion social structure. MRQAP tests the matrix equivalent of a linear regression and are widely used for hypothesis testing in networks (Farine 2017). We conducted a separate MRQAP for each pride in each season with association as the dependent matrices and age based homophily, sex based homophily and reproductive state based homophily as the independent variables. The homophily matrices were constructed by assigning similar pairs a value

of 1, while dissimilar pairs received a value of 0. We conducted these tests using the MRQAP function with a custom null model option in 'asnipe' package in the statistical software R (Farine 2013). The null model consisted of 10 000 permutations (see below)

To quantify the division of prides into subgroups and the nature of connections within prides and within subgroups, we used three network metrics: modularity, mean weighted degree and network density. Modularity describes the separation of networks into structural communities, or subgroups of individuals that are more connected among themselves than they are to others (Girvan & Newman 2002). Herein, we call these network-based communities "subgroups". A higher modularity implies that a group tends to break into distinct subgroups with stronger connections between individuals within a subgroup but weaker connection between individual in different subgroups (Newman 2004). Mean weighted degree is defined as the average sum of the weight of edges surrounding each node in a network; it measures the strength of connections among individuals in a group and a high mean weighted degree means most individuals were seen together most of the time. Network density is the ratio of the number of edges (nonzero edges) in the network over the total number of possible edges between all pairs of nodes. A high network density represents greater gregariousness among individuals with individuals being connected to more conspecifics. We represented the resulting subgroup assignments by giving different colours of nodes to each subgroup within a pride using the community detection algorithm (Fig. 1). All network measures were calculated in R using igraph (Csardi & Nepusz 2006).

Hypothesis testing

We first preliminarily tested for the correlation between the four measures of prey availability, and the correlations were generally moderate to low ($-0.59 \leq r \leq 0.62$), still each measure was analysed separately. All analysis were done in the statistical software R (Bates, Mächler, Bolker & Walker 2015) using linear mixed effects regression analysis and the identity link in the lme4 package. We assessed the relationship between the different network metrics (modularity, mean weighted degree and network density for each pride and subgroup network) and (i) the four measures of prey availability, (ii) a measure of interspecific competition (ratio of hyaena abundance to lion pride size), and (iii) a measure of vegetation cover (percentage of closed vegetation). The network metric was the response variable while the above ecological variables that can potentially influence lion social structure were the fixed effects; with lion pride ID included as the random effect. Using the null model procedure described below, we also generated 10 000 randomised versions of each network, and ran the same regression with each of these randomised networks. We then calculated P-values for each fixed effect by calculating the number of coefficients of the regression slopes from the randomised networks that were greater than or equal to the corresponding coefficient of the regression slopes using the observed network, divided by the number of random networks generated and corrected for a two-tailed test (Farine 2017). The regression coefficients were scaled (by subtracting the mean and dividing by the standard deviation) to make the strength of the effect comparable between the pride level and the subgroup level. All analysis were done in R statistical software (R Core Team 2019).

Null models

Social data are typically non-independent (Croft, Madden, Franks & James 2011), in order for one individual to have a connection, it requires another to do so as well. We used null models to estimate the statistical significance in the relationships between the ecological variables and the connections among individuals within prides and within subgroups. Null models allow us to account for confounding non-social factors that affect the observations of co-occurrences among individuals, such as sampling effort, so that only the signal of social factors that shapes the social network are evaluated when estimating significance (Farine & Whitehead 2015; Farine 2017). We first did a pre-network permutation test in the 'asnipe' package (Farine 2013) to compare the mean weighted degree, network density and modularity of the study pride networks to that of a random pride networks. Pre-network permutations work by sequentially swapping observations of pairs of individuals between groups for each iteration of the randomization to increasingly randomize the observed data (Bejder, Fletcher & Brager 1998). After each swap, the associations among all individuals are recalculated and the above three network measures recalculated. We conducted 10,000 such swaps, thus generating a null distribution from 10,000 randomised networks. We then re-ran the same null model procedure but restricted swaps to only occur within the subgroups that were identified within each network (i.e. within each pride). We calculated the mean weighted degree and network density for each subgroup networks and compared to that of random subgroup networks from the previous null model. Conducting this analysis allowed us to determine whether individuals are trading-off within-subgroup social investment versus pride-level social investments because in the first null model the associations were re-distributed across subgroups, whereas in the second null model the associations remained within subgroups.

Results

We first generated a baseline understanding of social structure in four lion prides by testing whether individual traits influence patterns of associations among individuals in replicated networks, each representing four months of observations in one of two dry seasons (see Methods). While there was a correlation between the individual trait (age, sex and reproductive state) similarity and the probability for individuals to be observed together (Table S2) in some prides, the adjusted R^2 value for the relationship between similarity in individual traits and association patterns among individuals within lion prides was generally low (except for Ngamo pride) (see Table S2).

We then tested whether prides exhibited structured patterns of subgrouping. We found that the seasonal networks for each pride could be statistically partitioned into two, three, or four subgroups (Table S3; Fig. 1). Season itself had no significant effect on modularity (the strength of division of a network into subgroups, estimate ± SE = -0.08 ± 0.13; t (7) = -0.62; p = 0.56). We then tested whether seasonally-varying ecological factors could explain patterns of structure, including subgrouping, in the networks.

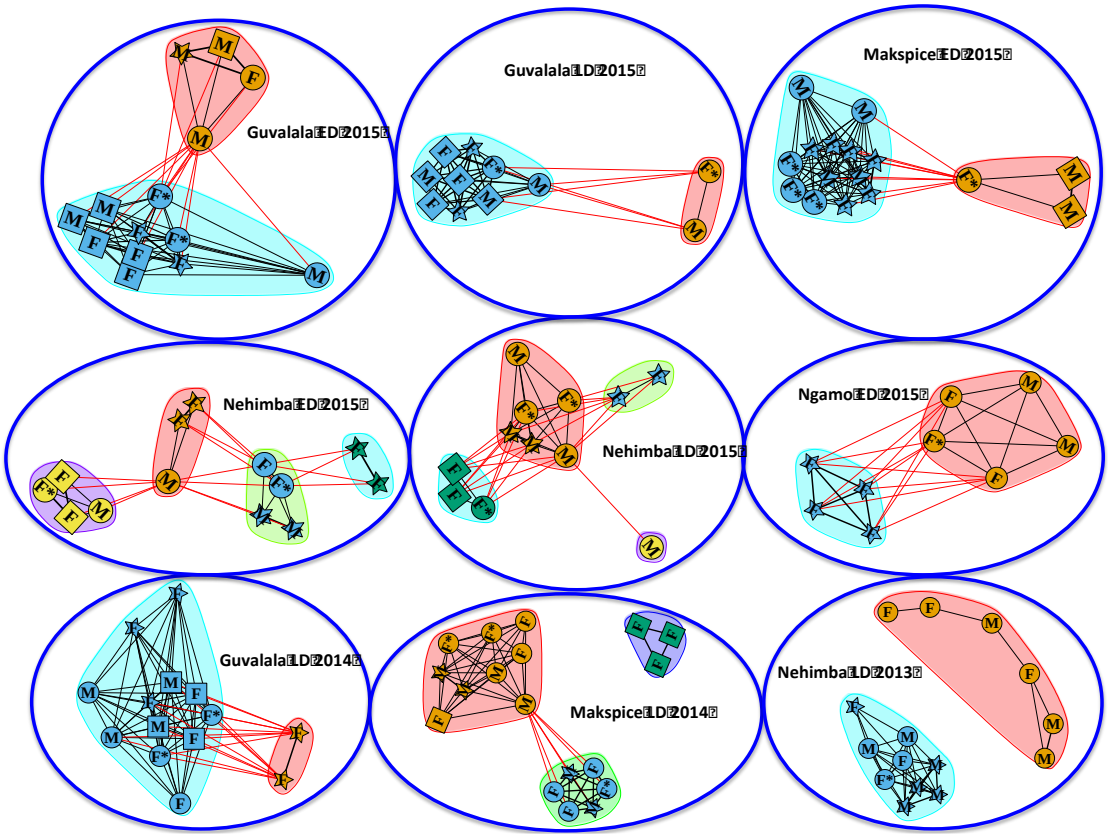
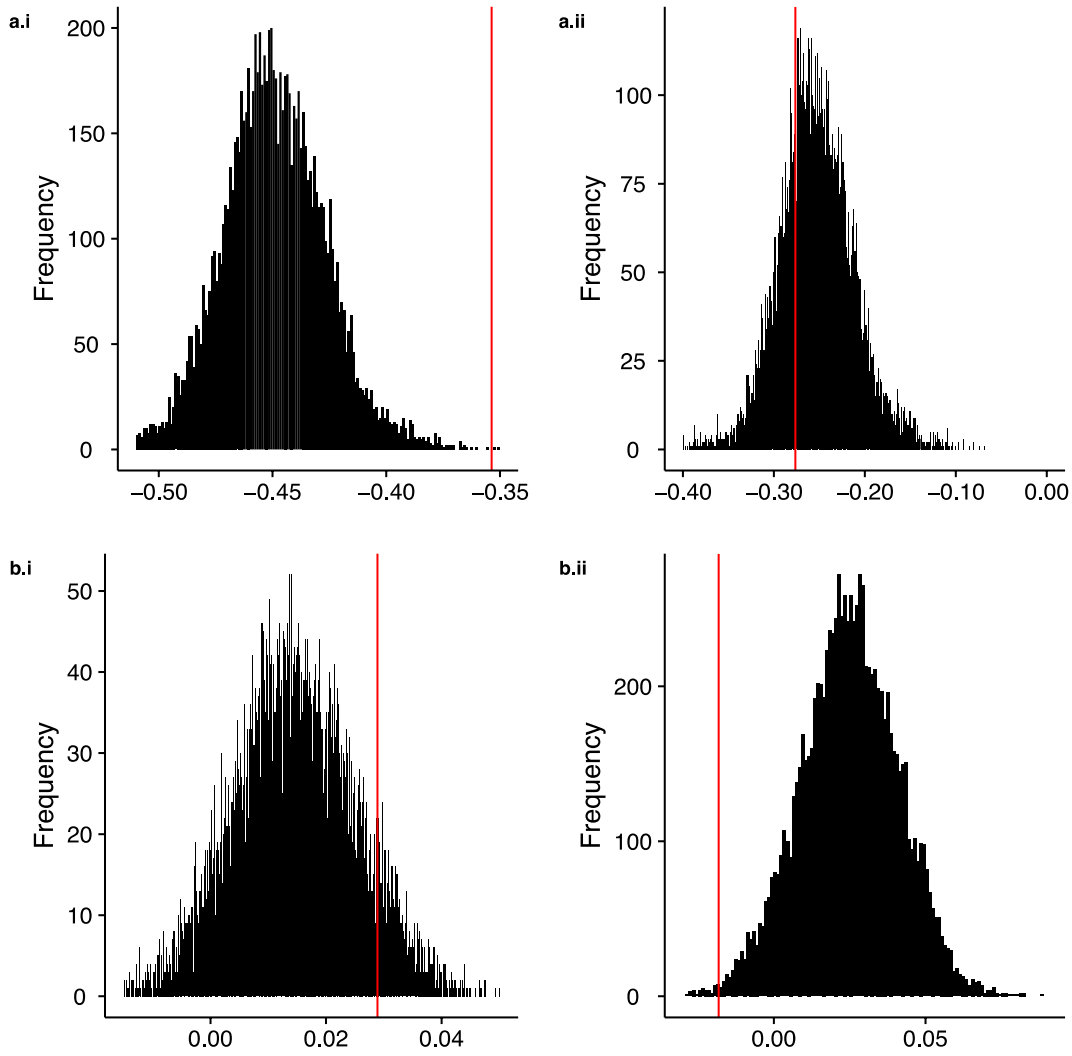


Fig. 1 Subgrouping patterns across a total of four prides, two distinct seasons (early dry season (ED) and late dry season (LD)) and three years (2013 to 2015). Pride identity, season and year are noted in each network. Each node, representing an individual lion, is assigned to a subgroup, which is denoted by node colour and coloured bubbles. The shape of the node donates lion age group (circle = adult, square = sub-adult and star = cub), the letter of the node indicates lion sex (M = male, F = female) and the * indicates the reproductive state (F* = females with cubs). Edge weights are proportional to the association index.

Prey abundance

The strength of division of prides into subgroups significantly increased (i.e. subgroups became clearer and more consistent) with increase in prey abundance (Table S4). Furthermore, the connections among individuals within prides became

384 significantly weaker with increasing prey abundance (Fig. 2a.i). However, this was
385 not significant when calculating strength of connections exclusively within subgroups
386 (Fig 2a.ii). Prey abundance had no significant effect on the gregariousness among
387 individuals (how many individuals were connected to, or network density) when
388 measured at the level of pride (Fig. 2.b.i) but an increase in prey abundance decreased
389 the gregariousness among individuals when measured at the level of the subgroups
390 (Fig. 2.b.ii; see Figure S1, Table S4, S5 and S6 for full results).
391



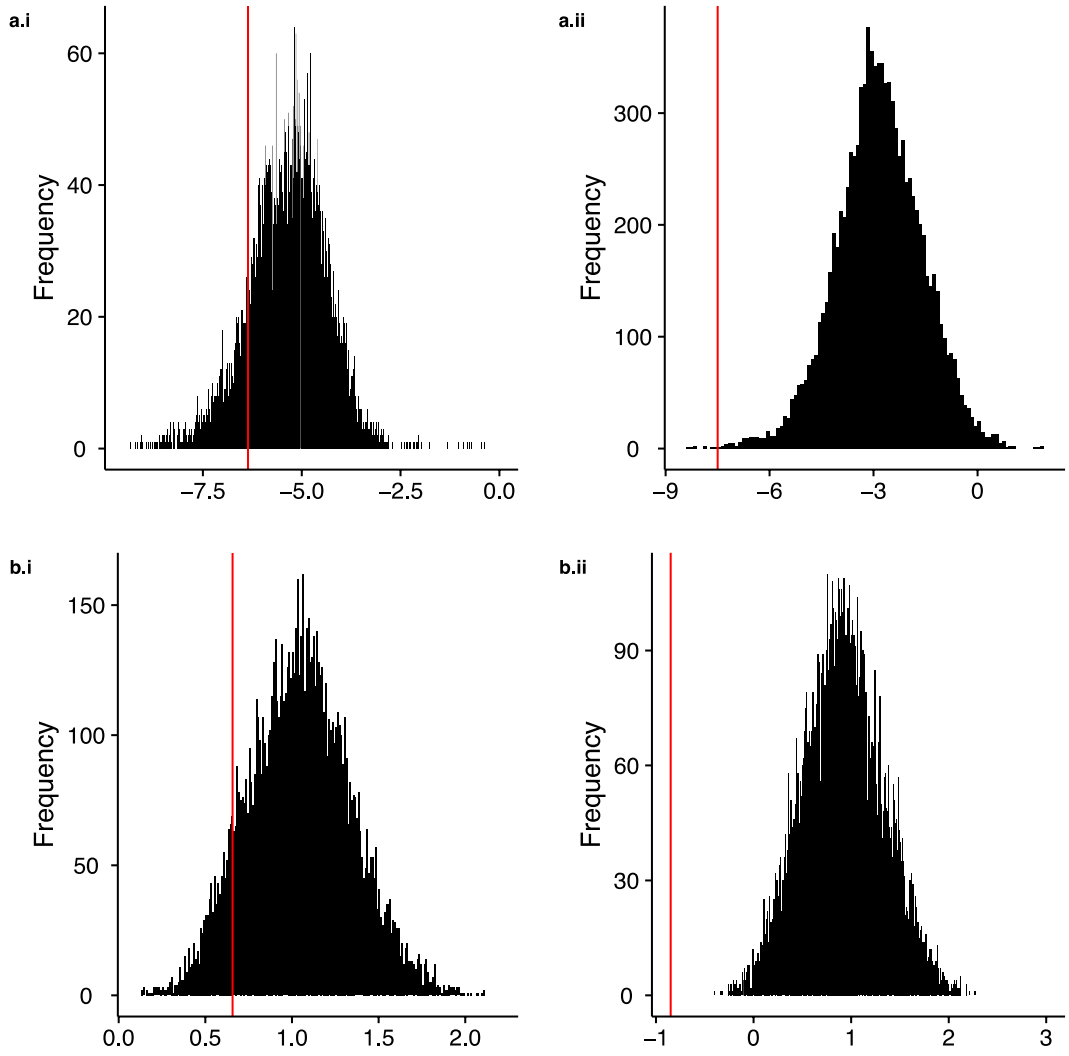
392

393 **Fig. 2.** The relationship between number of prey herds/km (index of prey abundance)
394 and a) mean weighted degree (strength of connections among individuals) within (i)

prides and (ii) subgroups and b) network density (gregariousness among individuals) within (i) prides and (ii) subgroups. The distribution of the coefficients of the regression slope of the random networks (black lines) and the observed network (red line).

Prey dispersion

The strength of division of prides into subgroups significantly increased (i.e. subgroups became clearer and more consistent, resulting in a higher modularity score) with increase in prey dispersion (Table S4). Prey dispersion had no significant effect on the strength of connections among individuals at the pride level, but significantly increased the strength of connections among members of subgroups (Figs. 3a.i and 3a.ii). Prey dispersion had no significant effect on the gregariousness among individuals when measured at the level of pride (Figs. 3.b.i) but an increase in prey dispersion decreased the gregariousness within subgroups (Figs. 3.b.ii; see Figure S1, Table S4, S5 and S6 for full results).



411

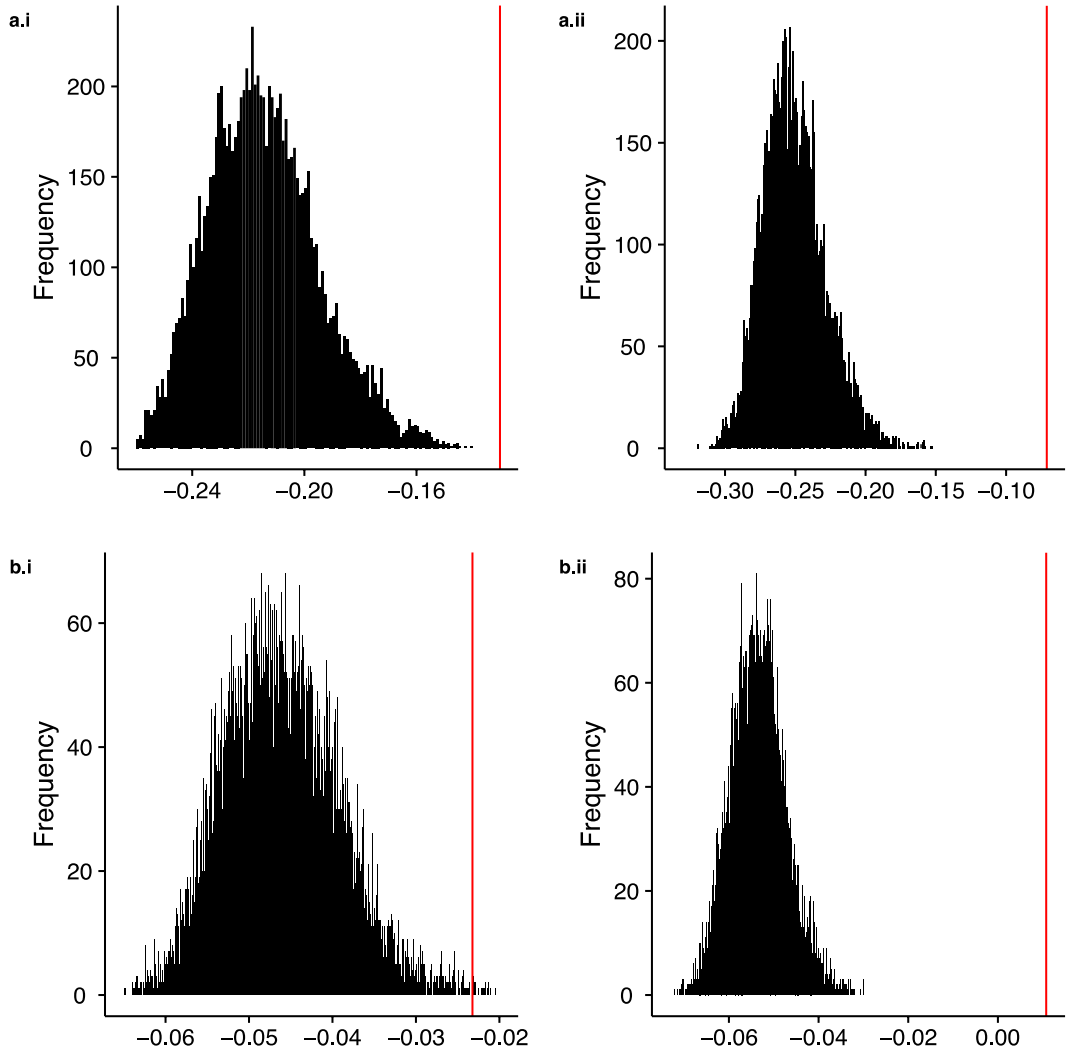
412 **Fig. 3** The relationship between nearest neighbour index of prey herds (index of prey
413 dispersion) and a) mean weighted degree (strength of connections among individuals)
414 within (i) prides and (ii) subgroups and b) network density (gregariousness among
415 individuals) within (i) prides and (ii) subgroups. The distribution of the coefficients of
416 the regression slope of the random networks (black lines) and the observed network
417 (red line).

418

419 *Patch richness (mean prey herd size)*

420 Mean prey herd size, an index of patch richness, had no significant effect on the
421 division of prides into subgroups (Table S4). The strength of connections among

422 individuals decreased at both the pride- and subgroup-level when prey herd size
423 increased (Figs. 4a.i; 4a.ii). Increase in prey herd size resulted in significant decrease
424 in gregariousness among individuals within prides (Fig. 4.b.i), and a significant
425 increase in gregariousness within subgroups (Fig. 4.b.ii; see Figure S1, Table S4, S5
426 and S6 for full results).
427

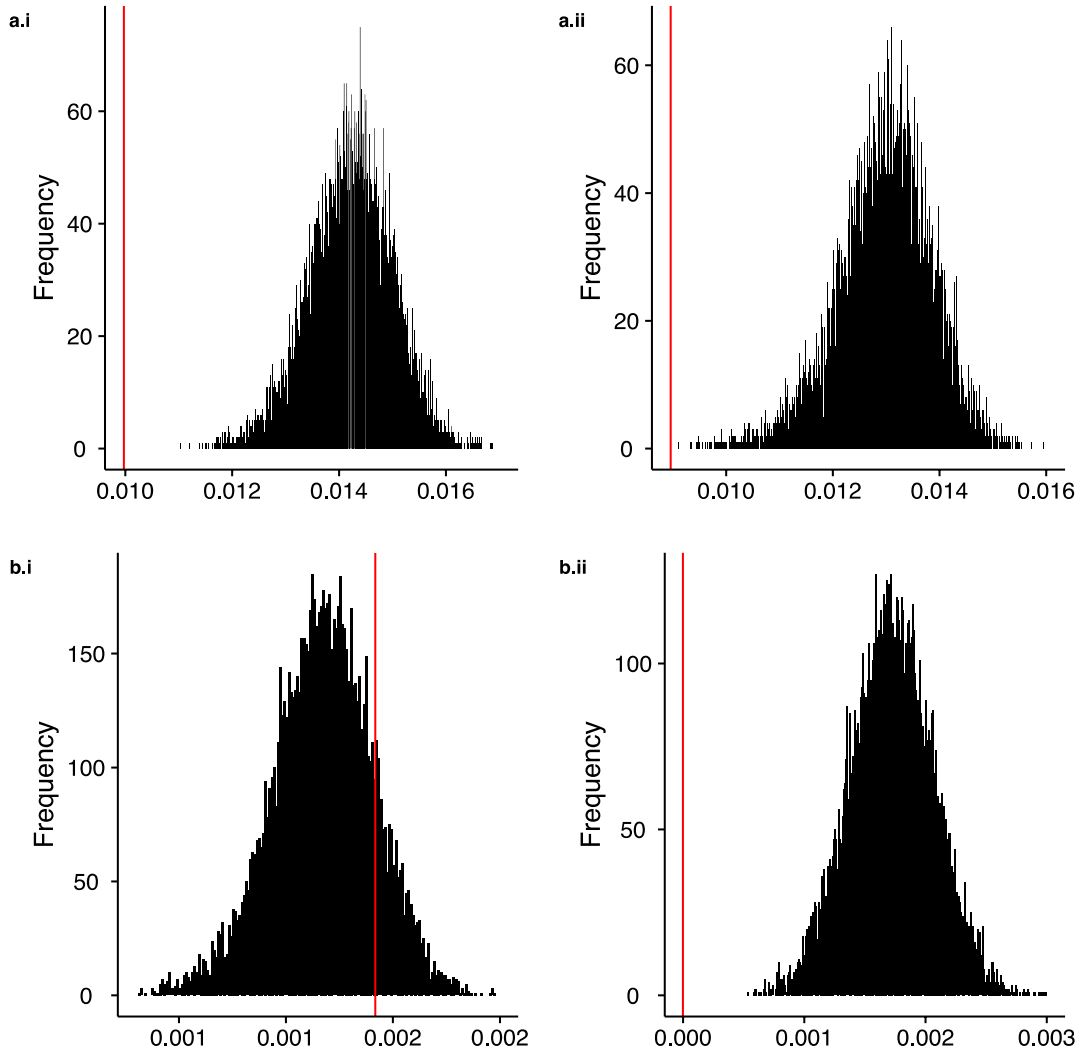


428
429 **Fig. 4** The relationship between mean prey herd size (index of patch richness) and a)
430 mean weighted degree (strength of connections among individuals) within (i) prides
431 and (ii) subgroups and b) network density (gregariousness among individuals) within
432 (i) prides and (ii) subgroups. The distribution of the coefficients of the regression

slope of the random networks (black lines) and the observed network (red line).

Patch richness (mean prey body size)

The strength of division of prides into subgroups decreased with an increase in mean prey body size, meaning that individuals tended to associate more evenly with all other members of their pride (Table S4). The strength of connections among individuals within prides and subgroups increased significantly with an increase in mean prey body size, with this effect being stronger within subgroups (Figs. 5a.i and 5a.ii). Mean prey body size had no significant effect on gregariousness when measured at the level of pride (Fig. 5.b.i) but an increase in mean prey body size significantly decreased the gregariousness among individuals when measured at the level of the subgroups (Fig. 5.b.ii; see Figure S1, Table S4, S5 and S6 for full results).



446

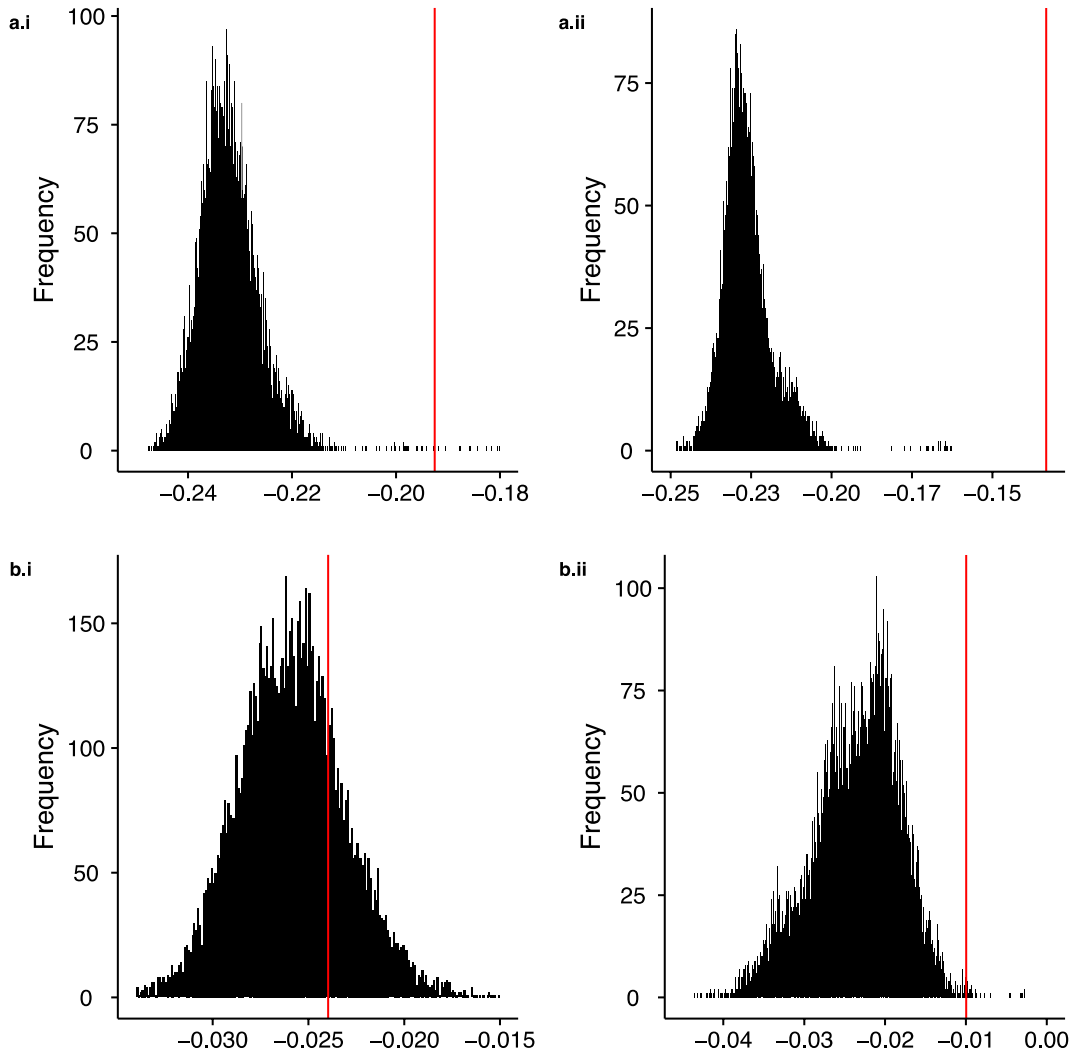
447 **Fig. 5** The relationship between mean prey body size (index of patch richness) and a)
448 mean weighted degree (strength of connections among individuals) within (i) prides
449 and (ii) subgroups and b) network density (gregariousness among individuals) within
450 (i) prides and (ii) subgroups. The distribution of the coefficients of the regression
451 slope of the random networks (black lines) and the observed network (red line).

452

453 *Interspecific competition*

454 The strength of division of prides into subgroups significantly increased (i.e.
455 subgroups became clearer and more consistent) with an increase in interspecific
456 competition (Table S4). The strength of connections among individuals significantly

457 decreased, for both pride and subgroups, when interspecific competition increased
458 (Figs. 6a.i; 6a.ii). Interspecific competition had no significant effect on the
459 gregariousness within prides (Fig. 6.b.i), but an increase in interspecific competition
460 significantly decreased the gregariousness among individuals within subgroups (Fig.
461 6.b.ii; see Figure S1, Table S4, S5 and S6 for full results).



462

463 **Fig. 6** The relationship between ratio of hyaenas to lions (interspecific competition)
464 and a) mean weighted degree (strength of connections among individuals) within (i)
465 prides and (ii) subgroups and b) network density (gregariousness among individuals)
466 within (i) prides and (ii) subgroups. The distribution of the coefficients of the
467 regression slope of the random networks (black lines) and the observed network (red

line).

Vegetation cover

Vegetation cover had no significant effect on division of prides into subgroups (Table S4). The effect of vegetation cover on the strength of connections among individuals was not significant either within prides or within subgroups (Figs. 7a.i and 7a.ii). An increase in vegetation cover resulted in a significant increase in gregariousness among individuals within subgroups (Figs. 7.b.i, 7.b.ii; see Figure S1, Table S4, S5 and S6 for full results).

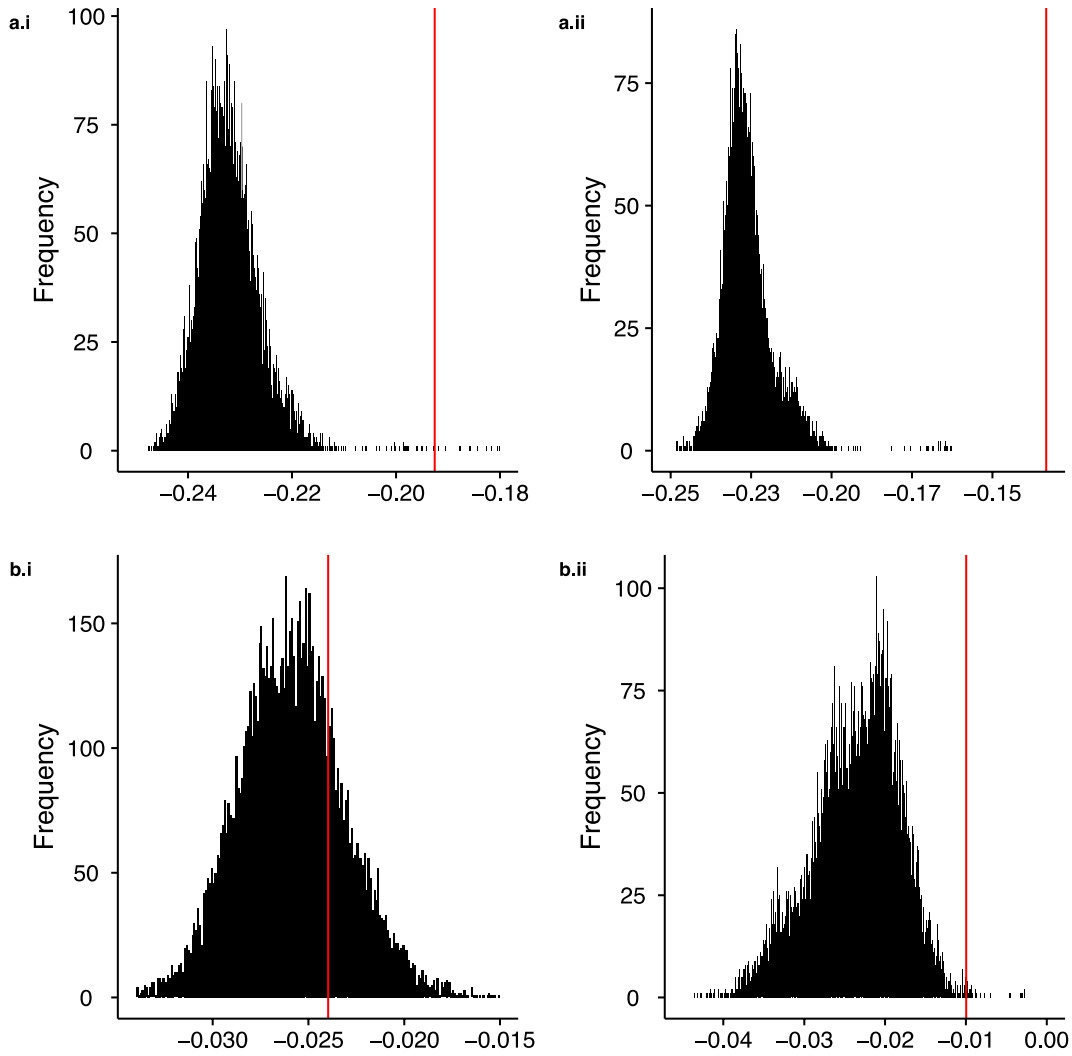


Fig. 7 The relationship between percentage of closed vegetation (vegetation cover) and a) mean weighted degree (strength of connections among individuals) within (i) prides and (ii) subgroups and b) network density (gregariousness among individuals) within (i) prides and (ii) subgroups. The distribution of the coefficients of the regression slope of the random networks (black lines) and the observed network (red line).

Discussion

Our study extends prior studies on the role of ecological factors in determining broad population structure by demonstrating their effects on the fine scale patterns of association among individuals at two scales: within groups and within subgroups. More specifically, our study revealed that an increase in prey abundance, prey dispersion, interspecific competition and a decrease in prey body size resulted in clearer and more consistent subgroups. These ecological factors also affected the strength, total amount, and variability in subgroup membership among individuals within a pride. Our study therefore provides evidence that ecological factors can shape both global and fine-scale properties of animal social systems, even when species live in seemingly consistently structured societies (e.g. with defined and long-lasting territories).

Individuals of similar characteristics often band together to form cliques, for example coalition males in cheetahs (*Acinonyx jubatus*) come together to increase their chances of holding territories (Caro & Collins 1986). Our network analyses captured some fundamental properties of lion behaviour, including the general propensity for lions to associate with individuals of the same sex. In lions, females often come

504 together to defend their cubs against nomadic males (Packer & Pusey 1983) whereas
505 males form coalition to take over and protect territories (Schaller 1972; Packer 1986).
506 However, overall our results suggest that the effect of individual trait similarity alone
507 explains relatively little of the variance in subgroup composition. One pride did show
508 consistent significant effects, but this is likely to be because this was a highly
509 gregarious pride composed of only adult males and females and their cubs, which was
510 quite unique to this particular pride.
511
512 Our key finding is that different axes of resource availability explained patterns of
513 social structure within groups and within subgroups. As the amount of available food
514 increased, prides tended to divide into subgroups. The excess available food might
515 provide individuals with an opportunity to invest more into strengthening bonds with
516 close associates within their subgroups rather than maintaining weaker bonds with all
517 pride members. Research in vampire bats (*Desmodus rotundus*) has highlighted that
518 strongly connected associates are the primary source of help when an individual is
519 going hungry (Carter *et al.* 2017). Subgroups of lions were also more gregarious when
520 food was scarce, capturing their tendency to maximize foraging efficiency by
521 searching in groups (Lachlan, Crooks & Laland 1998). Searching in groups is also
522 useful for sharing information about the resources as shown in other studies that
523 personal information and experience may be used to optimize search pattern and can
524 be useful in locating food patches (Aplin, Farine, Morand-Ferron & Sheldon 2012).
525 These results are in contrary to what Foster *et al.* (2012) discovered for killer whales
526 for which the associations between individuals in a group were stronger and the
527 network highly interconnected when food was abundant.
528

529 The dispersion of resources potentially increases searching behaviour (Sogard & Olla
530 1997; Valeix *et al.* 2010), thus limiting the opportunity for social interactions between
531 individuals at the pride level (Tanner & Jackson 2012). When resources are dispersed
532 across the landscape, prides tended to break into subgroups. We found that this led to
533 prides that were socially fragmented. Persistent separation between subgroups within
534 a pride reduces encounter rates and contacts among individuals across different
535 subgroups, which could have impacts on processes such as mate choice and other
536 social behaviours (Banks, Piggott, Stow & Taylor 2007; Krause, Lusseau & James
537 2009). Further, weaker associations between subgroups can make the pride less stable
538 (Beisner, Jackson, Cameron & McCowan 2011) and susceptible to other
539 anthropogenic and stochastic influences (Snijders, Blumstein, Stanley & Franks
540 2017). Recent experiments that involved temporarily splitting colonies of zebra
541 finches found that social instability increased social exclusivity (i.e. subgrouping)
542 and, as a result, decreased the collective performance of colonies in terms of foraging
543 efficiency (Maldonado-Chaparro, Alarcón-Nieto, Klarevas-Irby & Farine 2018).
544 When resource patches become more aggregated, for example through clustering of
545 prey herds in patches of specific habitats or around waterholes (Valeix *et al.* 2009),
546 lion prides tend to use these resource patches intensively (Valeix *et al.* 2010). This
547 aggregation of prey appears to allow regular associations among pride members,
548 leading to highly connected pride members with little subgrouping within prides.
549 Golden jackals (*Canis aureus*) have also been reported to aggregate around clumped
550 food sources resulting in a larger and more cohesive group (Macdonald 1979).
551
552 Prey herd size had no significant effect on the strength of the division of the pride into
553 subgroups, however the overall strength of connections among individuals, within

554 both prides and subgroups, decreased with increase in the size of prey herds. This
555 result is contrary to what we were expecting since larger prey herds can potentially
556 provide a chance for several predators within a group to make a kill or for more than
557 one individual to be killed from the herd (e.g. Creel & Creel 2002). Our results might
558 instead be interpreted in terms of lion foraging behaviour where both prides and
559 subgroups avoid hunting large prey herds because the increased vigilance by very
560 large groups reduces the attack success rate (Kenward 1978; Cresswell & Quinn
561 2011) which could make it difficult for lions to hunt successfully, especially buffalos
562 which have been known to mob predators and kill lions (Mangani 1962; Estes 1991).
563 In Serengeti lions have been shown to prefer smaller prey herds over large herds
564 (Scheel 1993).
565
566 We further found that the strength of division of prides into subgroups decreased with
567 increase in prey size. Large prey species (rich patches) such as buffalo, zebra, giraffe
568 or juvenile elephant can feed several lions, consequently, competition for prey within
569 the pride is likely to be minimal and individuals can associate frequently outside of
570 their close connections. Essentially, individuals in the pride tended to come together
571 more often (fusion), which could allow them to cooperatively hunt the large sized
572 prey (Scheel & Packer 1991) and increase success of prey capture (but see Caraco &
573 Wolf 1975; Packer *et al.* 1990) while minimizing energetic costs (Carbone, Teacher
574 & Rowcliffe 2007). Similarly, Kruuk (1972), and later Smith, Kolowski, Graham,
575 Dawes and Holekamp (2008), showed that when energy per resource patch is high,
576 hyaenas tend to congregate at such food patches and spend relatively more time with
577 conspecifics than alone. As a result the increased pride-level cohesion when prey is
578 large may also provide a number of other benefits to pride members, including

579 increased chances of communal defence of cubs (Packer & Pusey 1983) and territorial
580 defence (Grinnell 2002; Mosser & Packer 2009).
581
582 The strength of division of prides into subgroups increased with increase in
583 interspecific competition with the hyena. Furthermore, the gregariousness among
584 individuals in both subgroups and prides and the strength of their connections
585 decreased with increase in competition. This was contrary to our expectations of how
586 interspecific competition and predation risk would influence the fine scale animal
587 social structure. We expected cooperation to be higher and connections stronger
588 particularly in areas where there are higher densities of hyaenas as lions might need to
589 defend their kills from hyaenas (Cooper 1991). Perhaps our result is because the
590 cooperative mobbing behaviour by hyenas when they encounter lions (Lehmann *et al.*
591 2017) has the effect of weakening the bonds between individual lions and reducing
592 gregariousness.
593
594 As stalk-and-ambush hunters, vegetation cover has been shown to be an important
595 variable in the foraging behaviour and hunting success of lions (Funston, Mills &
596 Biggs 2001; Hopcraft *et al.* 2005) particularly for male lions (Loarie *et al.* 2013). In
597 our study, gregariousness among individuals within subgroups increased with
598 increase in vegetation cover. As expected of a stalk-and-ambush predator, lions would
599 spend more time and associate more with subgroup members, for a more coordinated
600 hunt in areas of good cover (Stander & Albon 1993; Hopcraft *et al.* 2005) where they
601 have a higher chance to successfully hunt prey like buffalo that are vulnerable to
602 predation in dense bush (Hay, Cross & Funston 2008).
603

The structure of the pride social networks, and the subgroups therein, captured the trade-offs individuals face between associating generally (equally across the pride) when resources are abundant and easy to find and catch, and associating more exclusively (in subgroups of preferred associates) when resources are scarce or more difficult to come by. Thus, we found seemingly consistent and predictable patterns of ecological factors on different aspects of within-pride social structure. However, the effect of ecological factors on the strength of connections and the frequency of associations among individuals were often more pronounced within subgroups than at the pride-level. Our results therefore suggest that the changes in pride structure under different ecological conditions can be dramatic from the perspective of individuals.

Our findings could be important given that individual lions are highly dependent on their pride mates for survival and reproduction (Packer, Pusey & Eberly 2001). Our results also suggest that increasing pride-level connectance with decreasing prey abundance is likely to arise from re-allocation of social associations from subgroups to other group members. This contrasts with a more traditional view of hierarchical societies in which higher-level organisation (here a pride) emerges from connections among more stable lower levels (here subgroups). Drawing on our knowledge of decision-making, our findings may insinuate that individual lions are making decisions at both the subgroup level and at the pride level.

A number of studies have examined the relationship between ecological factors and group size across a range of species, for example white-throated magpie-jays (*Calocitta formosa*) (Langen & Vehrencamp 1998), river dolphins (Gomez-Salazar, Trujillo & Whitehead 2012) and lions (Mbizah *et al.* 2019). Our findings suggest that

ecological factors can also influence the more complex fine-scale elements of social dynamics within groups. Decisions about sociality are often optimized to maximize individual fitness (Silk 2007; Farine, Montiglio & Spiegel 2015b) and in our study we found that individuals compromise between having few strong connections and having many weaker connections. These patterns mirror recent findings in vampire bats showing that individuals exhibit patterns of social bet-hedging, maintaining both stronger and weaker associations, which are differentially important in times of need (Carter *et al.* 2017). We further show that the trade-off is driven by different axes of variation in the underlying distribution of ecological resources. Our study therefore provides evidence that ecological factors can shape fine-scale properties of animal social systems at different scales, even when species live in structured societies that outwardly appear to be consistent.

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660

661 **Authors’ Contributions**

662 M.M.M., D.R.F., M.V., J.E.H., D.W.M., A.J.L. conceived the ideas and designed the
663 methodology; M.M.M. collected the data; M.M.M and D.R.F analysed the data;
664 M.M.M. led the writing of the manuscript. All authors contributed critically to the
665 drafts and gave final approval for publication.
666

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Supplementary Information Text

S1 Appendix

The spoor survey method

In this study prey availability was assessed using the spoor counting method, which is an indirect method of estimating population abundance. This method assumes that the intensity or frequency of animal signs is correlated to population size (Wilson & Delahay 2001). Spoor counting has been extensively used for estimating carnivore abundance (e.g. Funston *et al.* 2010), and has been found to be reliable for estimating abundance of large herbivores as well (e.g. Silveira, Jacomo & Diniz 2003). Multi-species spoor (animal track) count surveys were conducted from 2013 to 2015 during the early dry season and the late dry season. Roads or routes, termed transects, were divided into short segments, and these formed the units of the survey. Selected transects were driven and spoor were identified with the help of highly skilled and experienced trackers and care was taken to avoid double counting spoor. Vehicles driven at a speed of 10 - 15 $km.h^{-1}$ served as an observation platform during spoor surveys, with a driver, a recorder and a tracker sitting on a customized seat mounted to the front of a vehicle. Roads were not swept before the surveys and surveys were undertaken once per season for each of the five study sites.

When fresh spoor (less than 24h old) was encountered, it was assessed for species, herd size, age class and sex. The experienced trackers were able to determine if the spoor was fresh by the state and detail of the spoor, the shape and size of the spoor aided in determining the species, its age and sex, while the number of spoors around that area were counted to get the herd size. Only prey species and herd size were used in the analyses and we are confident that our highly skilled and experienced trackers could reliably assess these. Spoor were counted if they crossed transects but subsequent re-crossings were ignored when the trackers judged from the animal's movement patterns that these were apparently made by the same animal. During the surveys, spoor of a range of herbivores and carnivores were identified to the species level, but only spoor from lion prey species were used in this study. Prey species included in the analysis were Burchell's zebra (*Equus quagga*), giraffe (*Giraffa camelopardalis*), greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*), warthog (*Phacochoerus aethiopicus*), steenbok (*Raphicerus campestris*), common duiker (*Sylvicapra grimmia*), sable (*Hippotragus niger*), roan antelope (*Hippotragus equinus*), buffalo (*Syncerus caffer*), eland (*Taurotragus oryx*) and juvenile African elephant (*Loxodonta Africana*) (frequently recorded as prey during drought years in Hwange; Loveridge, Hunt, Murindagomo & Macdonald 2006).

S2 Appendix

Prey availability within lion home ranges

Lion home ranges were defined as the 90% probability contour of location distribution using the fixed kernel density estimator (Powell 2000) and the reference smoothing factor href (Hemson *et al.* 2005). Home range analyses was undertaken using the 'AdehabitatHR' package in the statistical software R (Calenge 2006). We used data from only one GPS collared lion per pride for each of the lion pride seasons. Prey availability data from spoor counts were overlaid on lion home ranges in QGIS (QGIS Development Team 2019) and the road transects that fell within each lion home range were clipped. For each home range and each season, we calculated four measures of prey availability, comprised of an index of prey abundance (number of

prey herds/km), an index of prey dispersion (nearest neighbour index of prey herds), and two indices of patch richness (mean prey herd size and mean prey body size). The nearest neighbour index was calculated in QGIS (QGIS Development Team 2019) by measuring the distance between each prey herd and its nearest neighbour and then averaging all these nearest neighbour distances. Prey body sizes were obtained from Cumming and Cumming (2003).

Figures

Ecological factors	Modularity	Weighted degree		Network density	
	Pride level	Pride level	Subgroup level	Pride level	Subgroup level
Prey abundance	***2.498***	***4.166***	-0.646	1.365	***-2.888***
Prey dispersion	***6.061***	-1.047	***-3.694***	-1.292	***-4.605***
Herd size	1.664	***4.165***	***7.708***	***3.269***	***11.655***
Prey size	***-7.443***	***-5.477***	***-4.507***	1.023	***-5.169***
Ratio hyena to lion	***4.231***	***6.547***	***12.435***	0.674	***2.721***
Vegetation cover	-1.387	-0.637	-1.408	-0.904	***-5.825***

Fig. S1 The scaled coefficients of the relationship between ecological factors and (i) modularity (strength of division of a network into subgroups), (ii) mean weighted degree (strength of connections among individuals) and (iii) network density (gregariousness among individuals). The bold and italics coefficients indicate significant relationships. For weighted degree and network density, the negative relationships become more negative along the blue gradient and positive relationships become more positive along the orange gradient.

982 **Supplementary Information Tables**
983
984 Table S1. Description of the factors that may influence lion social structure and the
985 four hypotheses tested in this study: (i) individual trait similarity, (ii) prey availability,
986 (iii) interspecific competition, and (iv) vegetation cover.
987

Description of Social and Ecological Factors
A. Social Factors
(i) Individual trait similarity
Sex - Grouping patterns of male lions may be influenced by their tendency to form coalitions that cooperate to compete with other coalitions for exclusive access to females (Packer & Pusey 1982). Grouping patterns of female lions is believed to be influenced by the need to protect their young and also maintain a long-term territory (Packer, Scheel & Pusey 1990).
Age - Age specific behaviour can also influence grouping patterns in lions. For example, subadult male lions may disperse from their natal pride and form coalitions with other dispersing subadult males (Van Orsdol 1981).
Reproductive state - In lions, lactating mothers tend to temporarily separate from the rest of the pride to forage and nurse their young (Packer *et al.* 1990).
B. Ecological Factors
(ii) Prey availability
Prey abundance - According to the prey abundance hypothesis, lions would be predicted to prefer areas of higher prey abundance (Hopcraft, Sinclair & Packer 2005), therefore individual lions may aggregate around these areas of high prey abundance
Prey dispersion - A measure of prey dispersion describes the distance lions have to travel to encounter prey or the effort involved in searching for prey. Lions would be expected to aggregate around areas of clustered prey patches, which are easily accessible (Valeix *et al.* 2010).
Prey herd size - A larger herd of prey might be considered a richer patch insofar as, all else being equal, it provides an opportunity for more than one lion to make a kill (in the Serengeti lions were observed sometimes to kill multiple prey when several lions attacked a herd and each captured an animal (Schaller 1972, page 251)) and also provides a higher chance of the lions finding a vulnerable individual within the herd. Larger preys herds are therefore expected to support larger lions groups.
Prey body size - A large bodied prey also might be considered a rich patch insofar as, for example, a single eland or giraffe could readily feed several lions, whereas a single gazelle could not. Availability of large prey would therefore promote large lions groups and strengthen group ties.
(iii) Interspecific competition
Hyaena to lion ratio - It is suggested that competition with hyaenas may impact the grouping patterns and social structure of lions (Cooper 1991). To avoid detection and encounters with hyaenas, lions may form smaller prides and also hunt smaller prey, so that they are less conspicuous (Périquet, Fritz & Revilla 2015). It is therefore likely that the ratio of hyaenas to lions may have an effect on lion social structure and grouping patterns.
(iv) Vegetation cover
Percentage of closed vegetation - As ambush predators, lions usually rely on cover when hunting (Hopcraft *et al.* 2005; Davidson *et al.* 2012). Dense vegetation would therefore provide cover for stalking lions and enable them to ambush their prey. The

increased chances of prey capture provided by the dense vegetation may increase the frequency with which individuals come together to hunt.

Table S2. Multiple regression quadratic assignment procedure (MRQAP) results for the effect of individual trait (sex, age and reproductive state (Repro state)) similarity on the connections among lions in a pride in the nine-pride seasons from 2013 to 2015. In bold are the significant P values.

Pride	Season/Year	Trait	β	P (β<=r)	P	R^2
Guvalala	Early dry 2015	Age	0.024	0.037	**0.073**	0.035
		Sex	-0.029	0.959	**0.082**	
		Repro state	0.173	0.000	**0.000**	
Guvalala	Late dry 2015	Age	0.188	0.001	**0.002**	0.012
		Sex	0.116	0.015	**0.031**	
		Repro state	-0.049	0.995	**0.009**	
Makspice	Early dry 2015	Age	0.067	0.058	0.116	0.035
		Sex	0.098	0.130	0.260	
		Repro state	0.033	0.102	0.204	
Nehimba	Early dry 2015	Age	0.043	0.131	0.262	0.030
		Sex	0.137	0.004	**0.007**	
		Repro state	-0.056	0.684	0.632	
Nehimba	Late dry 2015	Age	0.079	0.158	0.317	0.059
		Sex	0.136	0.003	**0.005**	
		Repro state	0.012	0.133	0.265	
Ngamo	Early dry 2015	Age	0.569	0.002	**0.004**	0.737
		Sex	0.180	0.000	**0.000**	
		Repro state	0.214	0.000	**0.000**	
Guvalala	Late dry 2014	Age	0.038	0.038	**0.077**	0.062
		Sex	0.075	0.242	0.484	
		Repro state	0.174	0.000	**0.001**	
Makspice	Late dry 2014	Age	0.142	0.046	**0.093**	0.062
		Sex	0.099	0.019	**0.038**	
		Repro state	0.013	0.851	0.299	
Nehimba	Late dry 2013	Age	-0.038	0.642	0.715	0.010
		Sex	0.015	0.332	0.663	
		Repro state	-0.193	0.899	0.202	

Table S3. The number of pride observations (Obs), number of individuals in a pride (Indiv), number of subgroups (Sub), and the three network metrics; modularity (strength of division of a network into subgroups), mean weighted degree (strength of connections among individuals) and network density (gregariousness among individuals) for each pride, per season, per year.

Pride	Year	Season	Obs	Indiv	Sub	Modularity	Weighted degree	Network density
Guvalala	2015	Early dry	66	14	2	0.24	3.39	0.60
Guvalala	2015	Late dry	45	11	2	0.04	4.95	0.65
Makspice	2015	Early dry	29	16	2	0.09	4.37	0.66
Nehimba	2015	Early dry	16	13	4	0.52	2.00	0.35
Nehimba	2015	Late dry	23	12	4	0.30	1.76	0.50
Ngamo	2015	Early dry	33	9	2	0.37	2.52	0.62
Guvalala	2014	Late dry	31	14	2	0.07	3.71	0.77
Makspice	2014	Late dry	23	18	3	0.56	3.19	0.35
Nehimba	2013	Late dry	26	15	2	0.16	3.00	0.32

Table S4. The coefficient (β), P value (P), range of random coefficients (range from, range to), mean and standard deviation (SD) for the relationship between ecological factors and modularity (strength of division of a network into subgroups). In bold are the significant P values.

Ecological factors	β	P	Range from	Range to	Mean	SD
Prey abundance	0.036	**0.008**	-0.133	0.0643	-0.0091	0.0182
Prey dispersion (PD)	0.266	**0.008**	-2.815	0.8430	-1.0000	0.4917
PD Without-outlier	3.235	**<0.001**	-1.167	2.9525	0.3392	0.4777
Herd size	0.045	0.114	-0.006	0.0638	0.0259	0.0112
Prey size	-0.003	**<0.001**	-0.003	0.0011	-0.0005	0.0004
Ratio hyaena to lion	0.023	**<0.001**	-0.006	0.0217	0.0064	0.0039
Vegetation cover	-0.010	0.176	-0.023	0.0004	-0.0065	0.0027

Table S5. The coefficient (β), P value (P), range of random coefficients (range from, range to), mean and standard deviation (SD) for the relationship between ecological factors and mean weighted degree (strength of connections among individuals) at the pride level and within subgroups. In bold are the significant P values.

Ecological factors	β	P	Range from	Range to	Mean	SD
Pride level						
Prey abundance	-0.354	**<0.001**	-0.539	-0.3504	-0.4494	0.0230
Prey dispersion	-6.360	0.272	-10.453	-0.3831	-5.3600	0.9548
Herd size	-0.130	**0.002**	-0.272	-0.0996	-0.2144	0.0202
Prey size	0.010	**<0.001**	0.009	0.0165	0.0141	0.0008
Ratio hyaena to lion	-0.193	**0.003**	-0.248	-0.1776	-0.2320	0.0060
Vegetation cover	0.094	0.464	0.079	0.1084	0.0962	0.0034
Subgroup level						
Prey abundance	-0.276	0.560	-0.432	-0.0683	-0.2535	0.0424
Prey dispersion	-7.497	**0.002**	-8.701	2.2460	-2.8376	1.2537
Herd size	-0.071	**<0.001**	-0.320	-0.1002	-0.2508	0.0226
Prey size	0.009	**<0.001**	0.009	0.0163	0.0130	0.0009
Ratio hyaena to lion	-0.133	**<0.001**	-0.248	-0.1629	-0.2263	0.0077
Vegetation cover	0.069	0.189	0.050	0.0942	0.0781	0.0066

Table S6. The coefficient (β), P value (P), range of random coefficients (range from, range to), mean and standard deviation (SD) for the relationship between ecological factors and network density (gregariousness among individuals) at the pride level and within subgroups. In bold are the significant P values.

Pride level	β	P	Range from	Range to	Mean	SD
Prey abundance	0.029	0.182	-0.025	0.0502	0.0145	0.0106
Prey dispersion	0.657	0.201	0.067	2.2194	1.0454	0.3004
Herd size	-0.023	**0.005**	-0.066	-0.0187	-0.0461	0.0070
Prey size	0.001	0.299	0.000	0.0020	0.0012	0.0002
Ratio hyaena to lion	-0.024	0.475	-0.036	-0.0150	-0.0259	0.0028
Vegetation cover	0.011	0.362	0.008	0.0173	0.0125	0.0014
Subgroup level						
Prey abundance	-0.018	**0.009**	-0.029	0.0966	0.0250	0.0162
Prey dispersion	-0.849	**<0.001**	-0.397	2.2734	0.9133	0.4126
Herd size	0.011	**<0.001**	-0.074	-0.0274	-0.0534	0.0061
Prey size	0.000	**<0.001**	0.000	0.0031	0.0017	0.0003
Ratio hyaena to lion	-0.010	**0.006**	-0.044	-0.0027	-0.0235	0.0055
Vegetation cover	0.006	**<0.001**	0.006	0.0189	0.0140	0.0014

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